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On the relationship between the number of ovules formed and the capacity of the ovary for maturing its ovules into seeds

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I. INTRODUCTORY REMARKS

In a series of papers published in part only and which need not be cited here, I have attempted by the use of the modern higher statistics to analyze the internal factors influencing seed production.

This work has consisted chiefly in determining the correlations between the degree of development of various somatic organs and the fertility of the fruit.

Certain peculiarities of the fruit itself have been also considered in their relationship to capacity for seed production or to the characteristics of the seed formed. A question of considerable interest upon which very little has been published is that of the relationship between the number of ovules formed by a fruit and its capacity for maturing these ovules into seeds. To the data of this problem the present paper is a contribution. In it only questions of fact will be considered, for it is quite premature to essay any interpretation of observed relationships in more general terms.

The problem in hand is to determine whether ovaries with a number of ovules above the average are more (or less) capable of developing their ovules into seeds than those below the average. *A priori*, ovaries with more than the mean number of ovules must be expected to produce on the average absolutely more seeds than those with less than the mean number. *A posteriori*, this condition is found almost without exception. But the question which interests the physiologist is whether ovaries of any class with respect to number of ovules are more capable of seed production as shown by their developing a higher proportion of their ovules into seeds.

This problem is not only of importance from the standpoint of the physiology of seed production, but of considerable interest from the fact that in *Staphylea* there is a selective mortality with respect to number of ovules, ovaries with a smaller number of ovules being less capable of developing into mature fruits than those with a larger number.*

The determination of the existence of such a relationship, especially the measurement of its intensity, presents considerable difficulty. It is desirable that degree of interdependence shall be expressed in terms of correlation, but there are dangers of spurious coefficients. Again, the work so far done has demonstrated very low correlations between somatic characters, or those of the fruit, and seed production. One would, therefore, anticipate very slight relationships between the number of ovules formed per fruit and its capacity for seed development. In such cases very large and numerous series of data are desirable.

II. METHOD OF ANALYSIS

I believe the following method of reasoning is valid.

In a series (a population, to use the technical term) of polyspermous fruits only a portion of the ovules develop into mature seeds. Let o be the number of ovules formed and s the number of seeds matured per fruit; both are variable; s is always some proportion of o. If there be no relationship between the absolute number of ovules formed and the capacity of the fruit for maturing its seeds, the most probable number of seeds for any pod is po, where

$$p = \bar{s}/\bar{o},$$

the bars indicating the mean value of the two variables. Now let $z = s - po$, or the deviation of any individual s from its probable value, on the assumption that the chances of an individual ovule developing into a seed are independent of the number of ovules in the ovary in which it is produced. The correlation coefficient between o and z, r_{oz}, should furnish the information we need.

A convenient formula for the determination of this relationship was most kindly worked for me while engaged on this problem at University College, London, by Professor Karl Pearson.*

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* Harris, J. Arthur, Biometrika **7**: 452–504. 1910; Science II. **32**: 519–528. 1910; Pop. Sci. Mo. **78**: 521–538. 1911.

III. DISCUSSION OF DATA

This formula has been so far applied to the problem of fecundity in plants only in the case of the fruits of *Cercis*, *Robinia* and *Sanguinaria* and of the inflorescence of *Staphylea*, *Celastrus* and *Crinum*.† Only one or two published series were available for each of these species. Because of the delicate relationships which are ordinarily found between fertility and other characters‡ it is essential for trustworthy results that the relationship be worked out on as large a series of material as possible. It will be also advantageous if one can include a large number of sub-series differing from each other in the conditions to which they have been subjected but each homogeneous in itself.

The only such series of data is that used for the working out of the relationship between bilateral asymmetry and fertility and fecundity in *Phaseolus vulgaris*.§ For each of these 53 series, embodying altogether over 170,000 pods, I have carried through the arithmetical routine necessary for the determination of r_{oz}, the correlation between the number of ovules formed per pod and the deviation of the number of seeds from their probable value on the assumption of there being no relationship between the number of ovules formed and the capacity of the pod for maturing its seeds.

TABLE I gives the results. The key letters indicating the individual series permit easy reference to other published information concerning them. The second column shows the number of pods upon which the determinations are based. The third gives the coefficient of correlation between the number of ovules and

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* Harris, J. Arthur, The Correlation between a Variable and the Deviation of a Dependent Variable from its Probable Value. Biometrika **6**: 438–443. 1909.

† For the results for the fruits of *Cercis*, and *Robinia* and the inflorescence of *Staphylea* see the original paper on methods. For *Sanguinaria* see Biometrika **7**: 321–324. 1910. For *Celastrus* see Missouri Bot. Gard. Ann. Rep. **20**: 116–122. 1909, and for *Crinum* see Missouri Bot. Gard. Ann. Rep. **23**: 85–89. 1912.

‡ For a review of the pertinent literature for plants see Biometrika **8**: 52–65. 1911.

§ Harris, J. Arthur, in Roux's Archiv. f. Entwicklungsmech. Organism. **35**: 500–522. 1912.

TABLE I

Series	N	r_{os}	r_{oz} and Probable Error	r_{oz}/Er_{oz}
L	1804	.374	−.040 ± .016	− 2.52
LL	8043	.357	−.014 ± .008	− 1.80
LG	806	.107	−.189 ± .023	− 8.27
BW1	346	.177	−.234 ± .034	− 6.82
BW2	467	.128	−.290 ± .029	−10.15
G	696	.542	−.012 ± .026	− .47
GG	6310	.247	−.102 ± .006	−17.25
GGH	5251	.461	−.101 ± .009	−10.98
GGH2	3502	.517	−.045 ± .011	− 3.94
GGHH	2656	.489	−.068 ± .013	− 5.20
GGD	1438	.362	−.069 ± .018	− 3.88
GGD2	1227	.426	−.020 ± .019	− 1.04
GGDD	807	.386	−.022 ± .024	− .95
H	5141	.444	+.012 ± .009	+ 1.23
HH	14029	.511	−.015 ± .006	− 2.68
HHC	2355	.504	+.121 ± .014	+ 8.82
HHH	11230	.426	−.057 ± .006	− 9.02
HHHC	2614	.501	+.101 ± .013	+ 7.69
HD	5581	.418	−.040 ± .009	− 4.47
HDC	1733	.509	+.086 ± .016	+ 5.32
HDD	5449	.500	+.026 ± .009	+ 2.87
HDDC	2308	.464	+.097 ± .014	+ 6.97
D	1473	.521	+.055 ± .018	+ 3.17
DD	1827	.496	−.046 ± .016	− 2.91
DDC	1159	.463	+.066 ± .020	+ 3.35
DDD	2018	.444	−.018 ± .015	− 1.17
DDDC	1542	.429	+.047 ± .017	+ 2.77
DH	5955	.548	+.029 ± .009	+ 3.29
DHC	2077	.409	+.045 ± .015	+ 3.05
DHH	5019	.446	−.052 ± .010	− 5.48
DHHC	2494	.438	+.055 ± .014	+ 4.06
USC	2569	.331	−.064 ± .013	− 4.79
USS	6605	.505	+.071 ± .026	+ 2.78
USSC	1888	.332	−.065 ± .016	− 4.21
USH	3406	.470	−.041 ± .012	− 3.60
USHC	1570	.322	−.091 ± .017	− 5.38
USHH	1743	.366	−.035 ± .016	− 2.18
USHHC	1936	.318	−.106 ± .015	− 6.95
USD	802	.376	−.018 ± .024	− .74
USDC	1810	.245	−.154 ± .016	− 9.91
USDD	851	.370	−.027 ± .023	− 1.17
USDDC	1619	.315	−.116 ± .017	− 7.05
FSC	2876	.344	−.056 ± .013	− 4.50
FSS	7809	.367	−.049 ± .008	− 6.42
FSSC	2457	.411	+.035 ± .014	+ 2.57
FSH	4541	.458	−.004 ± .010	− .38
FSHC	2117	.268	−.155 ± .014	−10.84
FSHH	3837	.398	−.028 ± .011	− 2.59
FSHHC	3180	.325	−.089 ± .012	− 7.43
FSD	1449	.433	+.002 ± .018	+ .12
FSDC	1506	.267	−.134 ± .017	− 7.83
FSDD	1556	.421	−.016 ± .017	− .92
FSDDC	2646	.328	−.101 ± .013	− 7.73

number of seeds per pod, r_{os}, while the fourth contains the correlations between the number of ovules per pod and the deviation of the number of seeds from their probable value.

All of the values for r_{os} are positive, and of a substantial order of magnitude. Both positive and negative coefficients for r_{oz} occur, and the values are low throughout. Of the 53 determinations, 38 are negative and 15 positive in sign. Were there no biological relationship between *o* and *s* an equal number of positive and negative values would be expected. Thus there is a deviation from equality of 11.5 ± 2.46,* which is probably significant.

Thus there is apparently a distinct negative relationship between *o* and *z*. This conclusion is supported by restricting the constants upon which it is based to those which are more probably statistically significant with regard to their probable errors. Thus I find that for the 41 constants 2.5 and more times their probable error 28 are negative and 13 are positive. Of the 26 constants which are over 4 times their probable error, 21 are negative and 5 are positive. Of the 13 which are over 7 times their probable error, 11 are negative and 2 are positive.

Taking means of the ratio of the correlation coefficients to their probable errors, I find a mean ratio of 5.10 for the negative values and of 3.87 for the positive. Thus the negative constants are as a whole more trustworthy than are the positive, although some of the positive values must be certainly regarded as trustworthy statistically.

Consider next the relative magnitude of the positive and negative coefficients. The 38 negative constants give a mean value of $-.0732$ while the 15 positive correlations give a mean value of $+.0529$. Thus the negative coefficients are numerically larger than the positive.

I now split the materials up into the individual varieties. The results are conveniently summarized in TABLE II.

Positive coefficients occur only in Navy, Ne Plus Ultra and White Flageolet. In the two latter, only 3 of the 22 constants are positive, and neither of the three can be safely regarded as significant with regard to its probable error. In Navy, quite different conditions seem to prevail. In both strains 6 of the 9 constants are positive. Numerically, the positive constants average higher than the negative, and in comparison with their probable errors they seem to be more trustworthy, the values of the ratio of r_{oz} to its probable error averaging higher in the positive than in the negative cases. Just the reverse of this condition is found everywhere else. All of the positive values which are over thrice their probable error fall in the Navy strains.

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* Calculated from $.6745\sqrt{53 \times .5 \times .5}$.

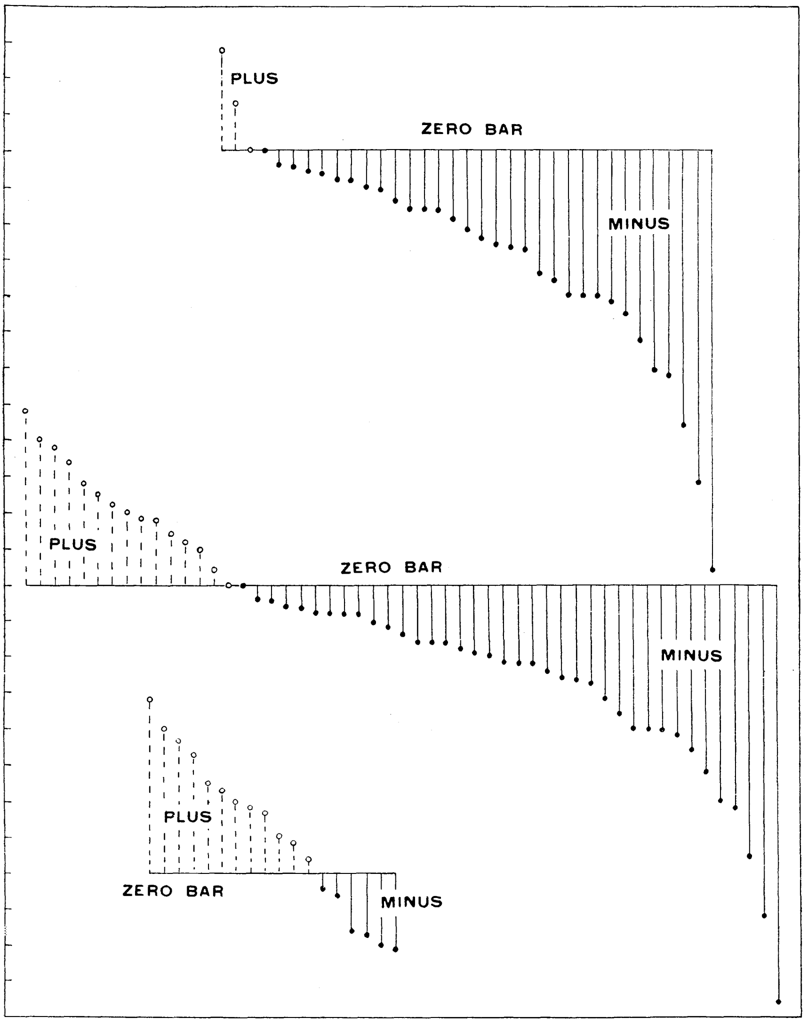

DIAGRAM 1. Intensities of correlation. One interval on marginal scale = .052.

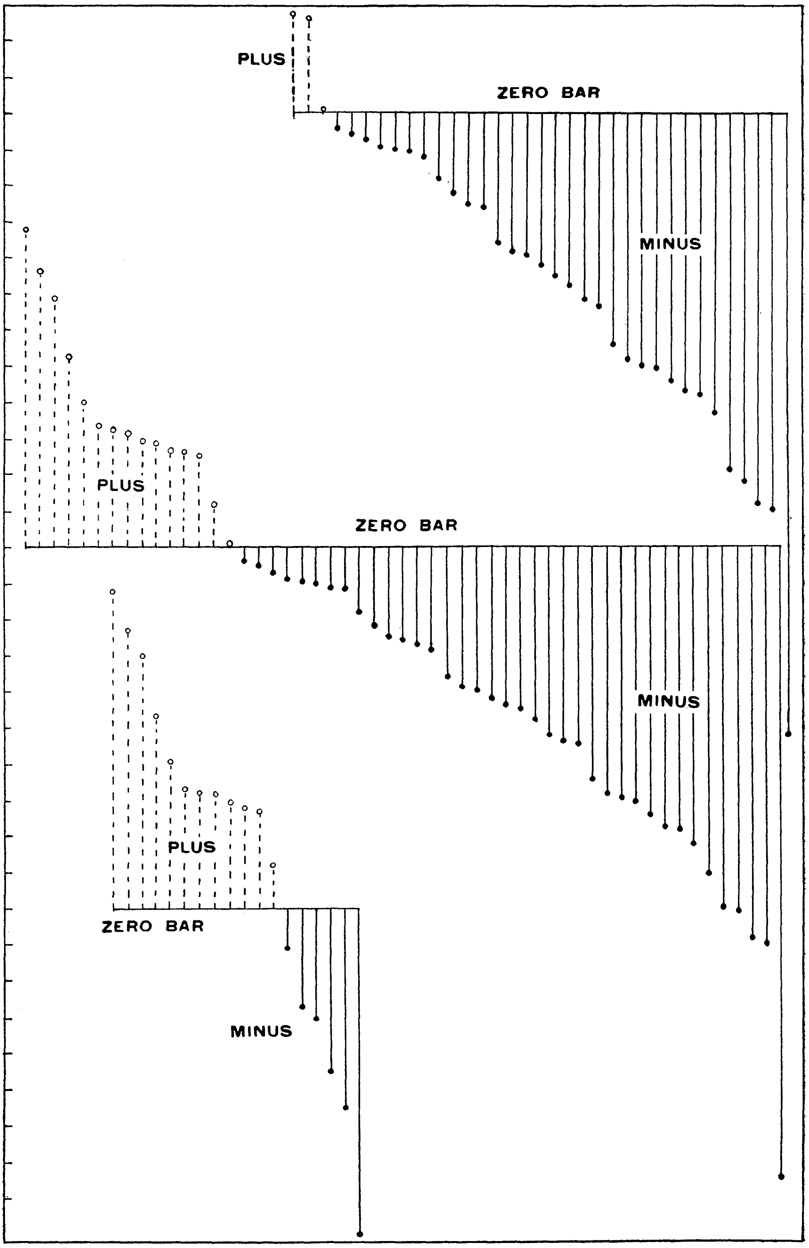

DIAGRAM 2. Significance of correlations as indicated by the ratio to their probable error. One interval on marginal scale = 1.

These relationships are forcibly shown in DIAGRAMS I and II. In both of these the intensity of the correlation is shown by the length of the vertical lines. The broken ones extending above the zero bar measure positive values; the solid ones extending below the zero bar indicate negative coefficients. In DIAGRAM I the lengths of the lines are in terms of the correlation coefficients, r_{oz}; in DIAGRAM 2 they are in terms of the ratio of the correlation to its probable error. In both, the large central figure represents the distribution of values for the whole material. This is analyzed into the Navy series, shown in the lower corner, and into all other series, shown in the upper right hand corner of the figures. The difference in the contribution of these two elements to the general series is very striking.

TABLE II

Variety	Number of cases	Mean r_{oz}	Mean $r_{oz}/E_{r_{oz}}$
Golden Wax			
Plus	—	—	—
Minus	3	−.081	−4.20
Black Wax			
Plus	—	—	—
Minus	2	−.262	−8.49
Burpee's Stringless			
Plus	—	—	—
Minus	8	−.055	−5.46
Navy H			
Plus	6	+.074	+5.48
Minus	3	−.037	−2.70
Navy D			
Plus	6	+.050	+3.28
Minus	3	−.039	−3.19
Ne Plus Ultra			
Plus	1	+.017	+2.78
Minus	10	−.072	−4.60
White Flageolet			
Plus	2	+.014	+1.35
Minus	9	−.070	−5.40

IV. RECAPITULATION AND DISCUSSION

In dwarf varieties of garden beans, *Phaseolus vulgaris*, there is but a slight relationship between the number of ovules per ovary and its capacity for maturing these ovules into seeds. So lax is this correlation that in working with only moderately large samples both positive and negative values of the coefficient may be found in the same strain of material.

Such a relationship does, however, exist. So far as the materials available may be considered as representative of the species it is generally negative, i. e., as the number of ovules formed increases the capacity for maturing these ovules into seeds decreases. This conclusion is supported by the facts that the negative correlations are significantly more numerous than the positive, they average larger numerically, and they have a higher degree of trustworthiness with regard to their probable errors.

In some varieties, however, the correlations seem to be generally positive. This is true for the common Navy. All other varieties so far as studied—White Flageolet, Ne Plus Ultra, Burpee's Stringless, Golden Wax and Black Wax—show exclusively or preponderantly negative correlations.

Concerning the explanation of this relationship no suggestion can be made. Such an attempt would be quite premature until ample quantitative data on the nature (sign) and intensity of the relationship in a considerable series of varieties are available. Anyone venturing to suggest explanations must also fully realize that the problem is an exceedingly complex one, involving many difficulties which need not be enlarged upon here. But as matters of biological fact the results seem definitely established, and represent one further step in the analysis of the problem of fertility and fecundity in plants.

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